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Mapping priorities for conservation in Southeast Asia

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ABSTRACT

Southeast Asian biodiversity is a global priority for conservation, due to the high levels of diversity and endemism, combined with some of the greatest levels of threat. Conservation planning is essential to ensure that hotspots of biodiversity and endemism have the protection needed to prevent deforestation, hunting and other forms of exploitation in some of the Southeast Asia's most diverse areas, yet this requires data which in many cases does not exist.

Growing volumes of online available data provides the ability to develop accurate models of species distributions, and gain new perspectives on regional diversity patterns and provide essential baseline data for planning and conservation.

Here, using the best available information I develop maps of the ranges of 2471 vertebrate (birds, mammals, reptiles and amphibians) and 1198 plant species, and explore patterns of biodiversity and the adequacy of protection. Each taxon shows different patterns of diversity, and no taxa provided an effective surrogate for diversity patterns in different groups. I show that for the majority of biodiversity hotspots fall outside protected areas, with between 10 and 55% of areas with at least >75% of the maximum number of species unprotected. The percentage of species ranges protected areas also varies by taxa, from a maximum of 40% to reptiles with a mean of only 13.5% of species ranges protected. Furthermore comparison between my predictions and IUCN maps of diversity differed greatly for all taxa examined, with IUCN hotspots covering a much larger portion of the region and potentially overestimating the ranges of many species. Further efforts are needed to better protect centres of diversity, and the inclusion of these methods into regional conservation planning may greatly assist in increasing the effectiveness of conservation.

1. Introduction

Southeast Asia is a global biodiversity hotspot (De Bruyn et al., 2014), however relative to other parts of the tropics there has been considerably less research across much of the Southeast Asian region (Martin et al., 2012). Southeast Asian biodiversity patterns are also highly complex, reflecting the complex biogeography of the region and demarcated and partitioned by a number of biogeographic divides (Hughes et al., 2011; Barley et al., 2015). The lack of baseline data, and limited surveys and inventories (both spatially and taxonomically) make assessing the efficacy of protected areas in protecting biodiversity highly challenging (Collen et al., 2008). In recent years the rate of species description across the region has continued to rise (Chapman, 2009), and groups analysed in detail show high rates of crypsis and taxonomic uncertainty, for example only around 50% of Southeast Asian bat species have officially been classified (Francis et al., 2010).

However the Southeast Asian region is also an undisputed hotspot of threat (Wilcove et al., 2013) and the global hotspot of threat to mammals (Schipper et al., 2008). The drivers of these threats are complex; however hunting and deforestation are among the most devastating to regional biodiversity (Hughes, 2017, Harrison et al., 2016). The region also has the highest rates of deforestation globally (Rosa et al., 2016) and some of the highest levels of landscape destruction and degradation of all global biodiversity hotspots (Sloan et al., 2014). This is especially troubling given the high regional endemicity and the potential loss of species given that Southeast Asia includes 4 of the 34 world biodiversity hotspots (De Bruyn et al., 2014).

For the majority of species across Southeast Asia there is no reliable source of range data (Verde Arregoitia, 2016), as no published data, or rigorous taxonomic data exists for the majority of species with a body size too small to be accurately be classified by camera traps (most rodents, insectivores, bats, amphibians and reptiles (Rovero et al., 2014; Ahumada et al., 2011, 2013; Beaudrot et al., 2016)). Developing regional priorities for conservation, or evaluating the adequacy of current protection on species relies upon having enough data on which to base these decisions. However with such high uncertainty in species

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distributions combined with rapid drivers of species loss; an evaluation of the adequacy of current protected areas is essential.

Multiple mechanisms have been advocated to develop these priorities, but the use of indicator taxa in the lieu of more complete knowledge of biodiversity patterns is one of the most widely utilised (Rodrigues and Brooks, 2007). Typically priorities have been based upon "charismatic" and easily fundable species such as the tiger (Smith et al., 2012), yet analysis shows that these "landscape species" are particularly poor surrogates of biodiversity (Jones et al., 2016). Therefore other methods to explore biodiversity patterns and develop appropriate targeted conservation strategies may be effective to the long-term survival of many species.

Given that no reliable maps exist for the majority of species, a possible way to make the best use of existing data is to collate distribution data and through combining it with environmental layers of various facets of the environment, to project the ranges of species across the region (Guisan et al., 2013; Platts et al., 2014). Once individual species distribution maps have been created it is possible to use these predicted distribution maps to ascertain centres of biodiversity, and then assay the adequacy of protected areas in these regions to explore the level of coverage and ensure that biodiversity hotspots are adequately protected. Endemism is another important point to be considered, and conserved; however mapping endemism relies on taxonomic data which does not yet exist for many of small mammal and amphibian species.

To secure a future for these species and ecosystems, protection is needed; both for biodiversity hotspots, and centres of endemism (Orme et al., 2005). Assaying the protected area coverage of biodiversity centres for these taxa is essential. Factors such as deforestation, hunting, mining, reservoir construction and numerous other factors act at higher rates and intensities outside protected areas on the majority of occasions, and as many of these species are already known from only small areas they are significantly at risk if their range does not fall within any protected areas (Li et al., 2016).

Here I explore how current knowledge of species ranges based on IUCN "expert drawn" maps compares to those produced through species distribution models and discuss the potential limitations, assumptions and challenges of both utilising both approaches. Using these two methods of exploring spatial patterns of biodiversity I compare the results, and explore the possibility of using any of the major taxa analysed (amphibians, birds, mammals and reptiles) as surrogate indicators for other taxa.

We also explore the distribution of biodiversity hotspots for four major vertebrate groups, in addition to non-flowering plants. Once biodiversity hotspots have been compared I then explore the level of protection, both for biodiversity overall and in terms of protected area coverage for each species for which sufficient data exists. Ultimately I discuss strategies for better protecting the biodiversity of one of the world's often forgotten biodiversity hotspots, and make recommendations for new spatial priorities and for sensitive approaches which provide a more effective mechanism for protecting regional biodiversity.

2. Materials and methods

2.1. Species distribution records

Distribution data for all taxa for the last two decades were downloaded from GBIF and cleaned to remove all suspect records for all birds, mammals, reptiles and amphibians for the mainland Southeast Asian region. Additional data for bats was included using the database compiled by Hughes et al. (2012), in addition to further data for China (Zhang et al., 2009, 2010). Duplicate records (i.e. repeated records of a species at a single locality) were removed from analysis, species with three or less points were also removed. Small sample sizes for species were included because this analysis seeks to optimise the retention of biodiversity by focussing on the most diverse areas, rather than on each species individually. Species range predictions using low numbers of localities will be conservative and are likely to be smaller than actual ranges, they may to a degree "cancel out" errors in other maps with similar errors, and will help define biotic hotspots. Once species with 1–2 records and duplicates (multiple captures of a species at the same site) were removed there was 12,928 records for 308 species of mammal (average 41.97 records per species) 14,642 records for 304 species of amphibian (average 48.16 records per species) 1941 records for 83 reptile species, and 286,603 records for 1820 species of birds. A selection of non-angiosperm plants were also analysed including 11,690 localities for 1198 species. Details of the exact number of records per family are available in Supplements 1.

2.2. Environmental layers

GIS layers for the whole of mainland Southeast Asia were compiled using a number of data sources, and scaled to 1 km resolution grids for the whole study area. Attention was made to try to include variables that sufficiently represented the conditions encountered by individuals of each species, to try to develop more "accurate" maps of each species distributions. During this analysis the following layers were used: aridity, potential evapotranspiration, a number of bioclimatic layers (bio1, bio12, bio13, bio14, bio15, bio2, bio3, bio4, bio5, bio6), canopy height, elevation, standard deviation of elevation variability using high resolution data, distance from karsts (digitised by hand for the region, and calculated using the path distance function in Arcmap), vegetation cover, humidity, lights at night (for 2012), net primary productivity (annual standard deviation in monthly primary productivity), population density, distance from rivers, and soil pH. Data sources are available in Supplements 2.

Environmental variables were selected to represent the conditions species experience based on their tolerances and dependencies. In the case of the bioclimatic variables I aimed to retain all factors which are likely to either be directly physiologically limiting, or to change access to important resources, whilst minimising the correlation between variables. Some bioclimatic variables are likely to show high levels of redundancy due to correlations between different bioclimatic variables. Therefore all bioclimatic variables were tested using a correlation matrix developed by using spatial principal component analysis in Arcmap. In cases where a variable was likely to have lower explanatory ability or relevance (i.e. minimum temperature of the coldest quarter compared with the minimum temperature of the coldest month) or correlated with a large number of other variables (i.e. daily temperature range) redundant bioclimatic variables were removed, and the remaining bioclimatic variables used (as listed above).

Initial vertebrate models showed bias due to increased sampling effort in the vicinity of roads (and thus correlated with lights at night), and as a result three vegetation layers were created to replace the lights at night layer and better elucidate the relationship between species and habitat requirements, whilst minimising observer biases. Three "vegetation intactness" layers were created, percentage coverage of forest per km^2, distance to forest and mean tree density per km^2.

Forest was mapped using continuous 30 m resolution tree density data (Sexton et al., 2013) combined with road data (open street map) and deforestation data (Global forest watch: www.globalforestwatch.org). 30 m resolution continuous tree cover data was downloaded from 2005 imagery data and tiled using the "mosaic to new raster" function in Arcgis. Areas which had been deforested between 2000 and 2014 and roads were then removed using spatial analyst tools. Three different vegetation layers were then created from this updated 2014 tree density map. To create a forest layer the continuous tree-cover layer was reclassified to forest and non-forest using 60% tree density as a minimum threshold to signify forest cover. This threshold was selected because when maps of rubber (Li and Fox, 2012) were used to test for adequate separation tree density of forest relative to rubber densities below this gave a high rate of misclassification of rubber as forest. With a 60% threshold to delineate forest misclassification drops to only 1% at a 30 m resolution.

A tree density layer was created using the 2014 tree density map and using the block statistics to determine the mean density in blocks of 33 × 33 cells before converting to a 1 km cell size of average tree density. The remaining two layers utilised the binary forest-non forest data to give a "distance to forest" layer (using distance tools) and a "Percentage forest coverage layer" by giving forest a value of 100 and non-forest a value of 0 and taking the mean for each 33 × 33 block before converting to a 1 km resolution. These three layers encapsulate dimensions of forest access and intactness without the observer biases associated with the lights at night layer.

2.3. Modelling

Species distribution models were run using Maxent (Phillips et al., 2006; Phillips and Dudík, 2008) using the default parameters, for all vertebrates species three replicates were run and the average of the three models used for further analysis. Maxent was selected as it has been found to show a higher predictive ability than the majority of other species distribution models, and to produce more accurate outputs than many other modelling approaches, even with small datasets (Merow et al., 2013; Ortega-Huerta and Peterson, 2008). Furthermore as absence data cannot be reliably collected for the majority of vertebrate species and as Maxent relies only on presence data it is an ideal way of utilising this data.

After initial models were run and analysed (which included lights at night layer as an input variable) all vertebrate were rerun using the three additional vegetation dimensions layers instead. Though some species will avoid disturbed areas this should be captured through looking at their relationship with vegetation alone (as the four metrics of intactness of vegetation cover are included (including canopy height)), without the inclusion of observer bias which may correlate with the use of anthropogenic layers (a particular issue for birds, as most observations are gathered by non-specialists).

Output species occurrence maps were reclassified to produce a binary presence-absence map for each species using the 10% training presence threshold. The 10% training presence threshold was utilised because it has frequently been found to be the most accurate and conservative threshold for delineating suitable from unsuitable areas (Escalante et al., 2013; Kramer-Schadt et al., 2013; Radosavljevic and Anderson, 2014). Once analysis and reclassification was complete binary maps for all species within each of the five taxonomic groups were combined to yield a diversity map for each taxa which showed the number of species any area is suitable for using the mosaic to new raster function.

Each of these maps was then reclassified to show areas with at least >50% and >75% of maximum diversity (i.e. if 100 species was the maximum number of coexisting species within a taxa within, then the >50% richness value would be 50 species, and the >75% value would be 75 species). These modelling hotspot maps were then overlaid with the protected areas map for Southeast Asia (using maps produced by protectedplanet: www.protectedplanet.net/) to calculate what percentage of these diversity hotspots are currently protected.

The percentage of each species' range within and outside protected areas was calculated to explore how well different taxonomic groups are protected at present. Non-angiosperm plants were used to examine diversity patterns, but individual ranges were not examined in detail due to small sample sizes, and taxonomic uncertainties in data collection.

Richness maps were also developed for species with different IUCN redlist statuses, though many reptile species are currently "under review", and have no assigned status. Additionally endemism was explored using the SDMTools toolbox, and biogeographic zones were examined through spatial principal components analysis, and maximum likelihood classification.

2.4. IUCN distribution data

Modelled species distributions were then compared to IUCN and Birdlife species distribution maps (http://www.iucnredlist.org/technical-documents/spatial-data; http://www.birdlife.org/datazone/info/spcdownload). Join by field was used to select the IUCN data to an index of the species included in the study, and the shapefiles clipped to match the study area. The "Count Overlapping Polygons" toolbox was then used to obtain IUCN species richness at a 1 km resolution and the diversity compared to the output of the models. The difference between model predictions and IUCN richness data were then explored, in addition to the distribution of IUCN hotspots (based on the >50% and >75% diversity thresholds) relative to those from models.

3. Results

3.1. Biodiversity patterns

A maximum of 128 mammals, 632 birds, 330 non-flowering plants, 30 reptiles and 65 amphibians were projected to inhabit any specific 1 km^2 grid cell (Fig. 1, bird family richness Supplements 3). Diversity hotspots for the four vertebrate orders considered showed considerable congruence in remaining forested areas, especially those in forested areas of Vietnam, the Thai Highlands in Chiang Mai and forested areas in Peninsula Thailand and Malaysia. Most groups additionally show high diversity in forested areas of west Myanmar, despite lower sampling intensity for many taxa in this region.

Drivers of diversity (Supplements 4) show marked similarities between taxa, with the most influential factors often being shared across taxa. Temperature seasonality is one of the most influential traits overall (12.4% on average), followed by land-cover (10.4%), and these two factors in addition to altitude also had the greatest variation in their relative influence in determining species distributions.

Modelled diversity showed large differences from IUCN maps for amphibians and mammals (Fig. 2, Supplements 5). Part of this difference may be due to the incorporation of rare species in my analysis, many of which are currently "under review" by the IUCN, and for which no map is available. Consequently the IUCN maps may show biodiversity patterns more accurately for generalist and wide-ranging species, but may potentially undervalue areas with high levels of endemism. IUCN maps also classify a much larger region as maximum biodiversity for all three vertebrate taxa (amphibians, birds and mammals, IUCN reptile maps are not currently available: Fig. 2, Supplements 5) compared to modelled projections, indicating that species ranges within IUCN spatial data are considerably larger than those generated by predictive models, and again potentially limiting the ability of IUCN maps to sensibly inform conservation prioritisation.

According to the IUCN maps mammals 38.4% of the region is classed as >50% of diversity, 30.6% in birds and 30.2% in amphibians, whereas the model only predicts 4.76%, 1.13% and 0.87% respectively of the region to have >50% of diversity. At >75% diversity the disparity is equally high at 13.6% of the land area classified in the top >75% of diversity for mammals according to the IUCN, 43.5% for birds and 4.1% for amphibians compared to only 0.36% for mammals, 0.01% for birds and amphibians based on my analysis. Thus the models defined areas of maximum richness are a fraction of the size of those indicated by the IUCN maps, suggesting much higher turnover in species in predictive analysis than in IUCN expert drawn range maps (Fig. 2, Supplements 5). The fact that the IUCN hotspots do not match those of models, indicates that the use of IUCN maps for species or ecosystem level prioritisation may be difficult due to the over-prediction and generalisation of species ranges in IUCN maps.

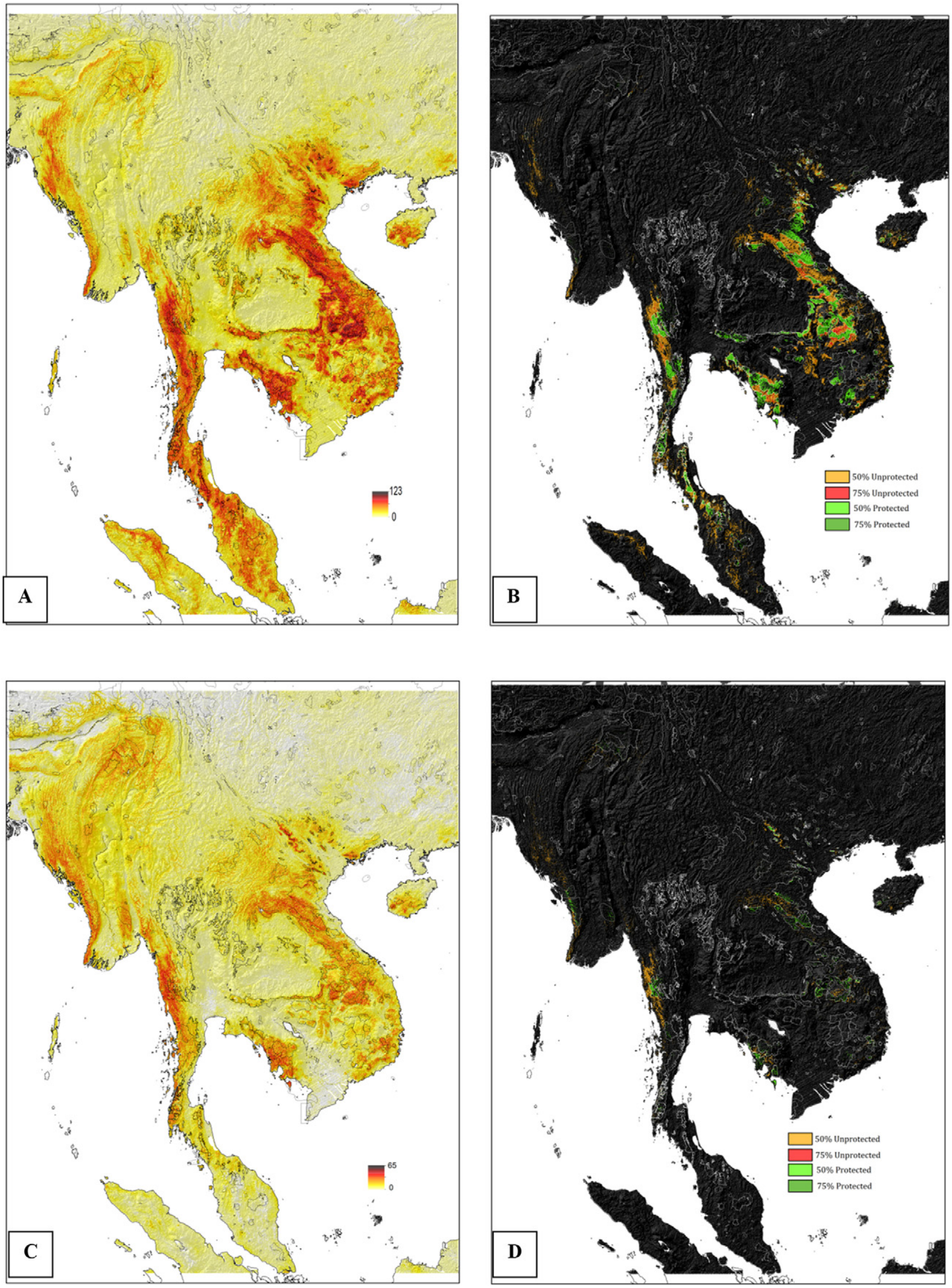

Fig. 1. A–B Mammals, C–D amphibians, E–F birds, G–H reptiles, I–J plants (non-angiosperms). Predicted richness for each group is shown (A, C, E, G), and regions with >50% and >75% of the greatest number of species within and outside protected areas (B, D, F, H).

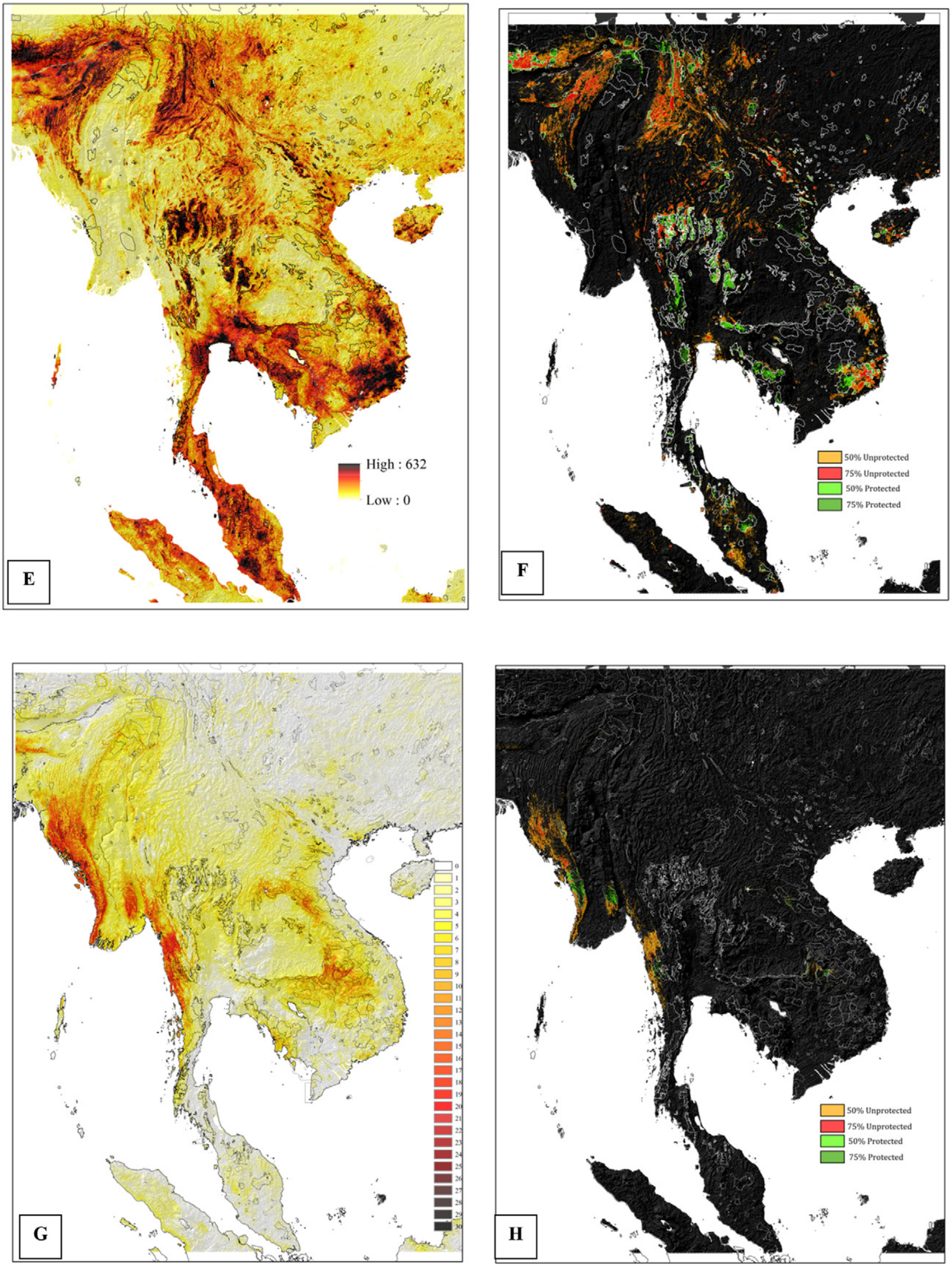

Fig. 1 (*continued*).

Areas of maximum diversity vary between the two approaches with 33% of the area modelled as having at least >50% of maximum diversity and 14.5% of areas modelled as having at least >75% of diversity amphibians falling outside IUCN hotspots. Birds and mammals also have portions of diversity hotspots falling outside IUCN hotspots (birds: 2.1% at >50%. 4.7% at >75% diversity, mammals 0.2% at >50% of diversity and 5% of areas with >75% of diversity).

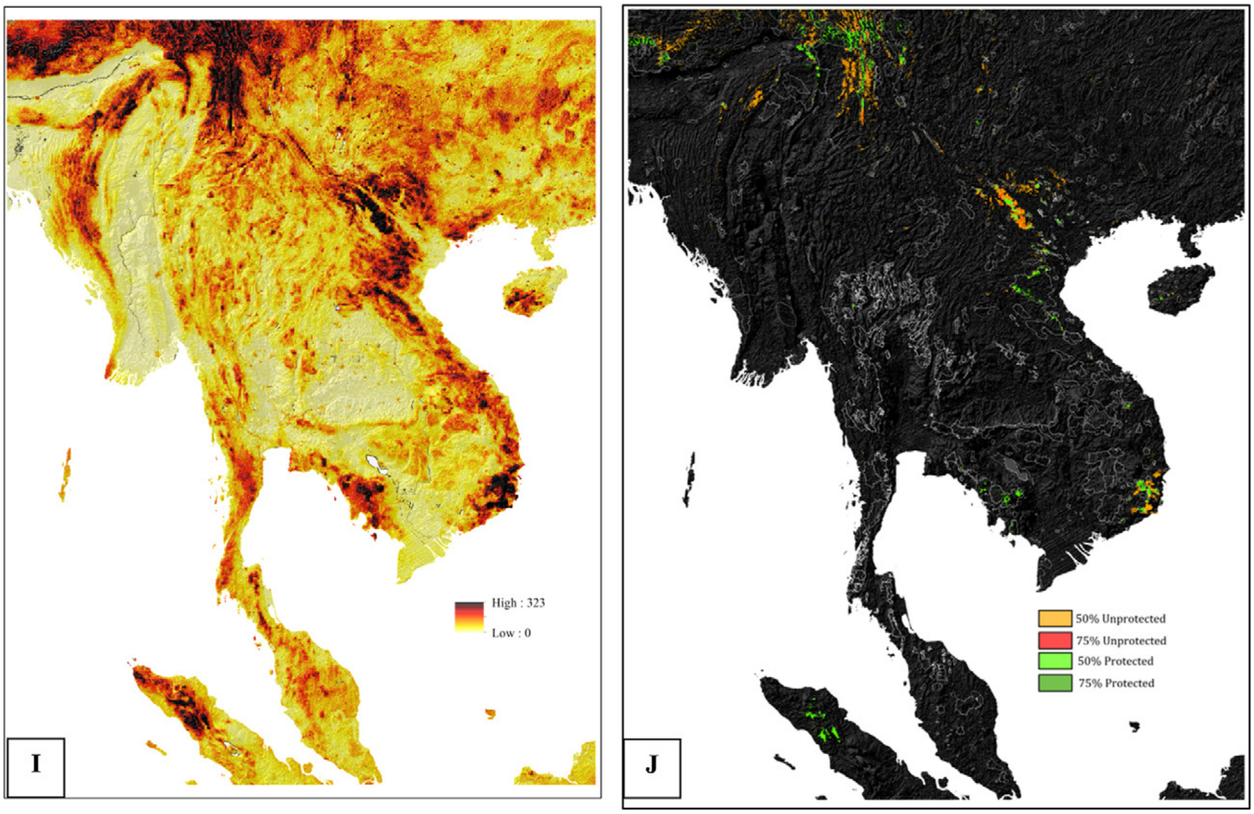

Fig. 1 (*continued*).

3.2. Indicators of biodiversity

Between the four vertebrate groups considered in models there are considerable differences between the hotspots for each taxa, and relatively little overlap between hotspots for several of the groups (Supplements 6). For most taxa the majority of their diversity hotspots do not overlap with those of other taxa, as a result at >50% maximum diversity 87.9% of bird, 87.3% of mammal hotspots and 77.2% of reptile hotspots to not overlap with those of any other vertebrate groups (only 13.2% of amphibian >50% hotspots).

At >75% diversity there is slightly more overlap with other taxa; for reptiles (63% non-overlapping) mammals (55% non-overlapping) and amphibians (3.5% non-overlapping) but in birds the figure increases to 92.8%. However, amphibians do show a substantial overlap between their diversity hotspots and those of other taxa; most notably reptiles and mammals. The small proportions of ranges overlapping is also likely to relate to the very small region with the highest levels of biodiversity, whereas as Fig. 1 shows, areas with high levels of diversity are largely shared between taxa, especially between mammals, reptiles and amphibians.

3.3. Diversity and threat

Political boundaries are also visible on IUCN species richness maps, especially for amphibians and mammals (Hughes, in review). According to IUCN maps species richness can halve just across a political border ((i.e. amphibian richness drops from 44 to 20 species on the Southern Yunnan border between China and Lao) see Fig. 2) reflecting problems in methodologies used to develop IUCN distribution maps rather than actual differences in diversity across such short distances. This relates to a shortcoming in IUCN methodology which will not extend species ranges into countries where they are not listed, but if there is no knowledge on the real range boundaries a political border provides a convenient delimiter.

The level of endangerment also does not relate linearly to diversity (Supplements 7–8), and the proportion of species with different endangerment statuses varies regionally. Within the amphibians the proportion of data deficient species is highest in the northernmost parts of the study area, in Northern Myanmar, Southern Tibet and areas of Southern Yunnan. Areas of Sumatra also have a high percentage of both endangered and data deficient species and Peninsular Malaysia also has a high proportion of endangered species. Other endangerment statuses are at low levels across the study region, though greater total numbers of species are within forested areas across the region. Within mammals there is also a higher proportion of data deficient and endangered species in northern parts of the region, where species richness is lower. Within birds a rather different pattern exists, with species of least concern dominating communities in most of the region, but with much higher proportions of endangered and threatened species in most intact forested areas, especially in Cambodia-Southern Lao and Southern Vietnam and Peninsula Malaysia.

Endemicity patterns also vary taxonomically and spatially (Supplements 9). Birds show their highest endemism in the Andaman Islands, but also show high levels of endemism across Peninsula Malaysia and in Lao Cai in Northern Lao. Amphibians also show high levels of endemism in Lao Cai, in addition to Modog in Southern Tibet. Reptile endemism peaks in areas of Myanmar, whereas mammals show high levels of endemism in certain forest regions where their diversity is also high, but particularly in parts of Vietnam.

3.4. Protection

In terms of biodiversity protection and species protection; protected areas do not currently cover some of the most diverse areas in the

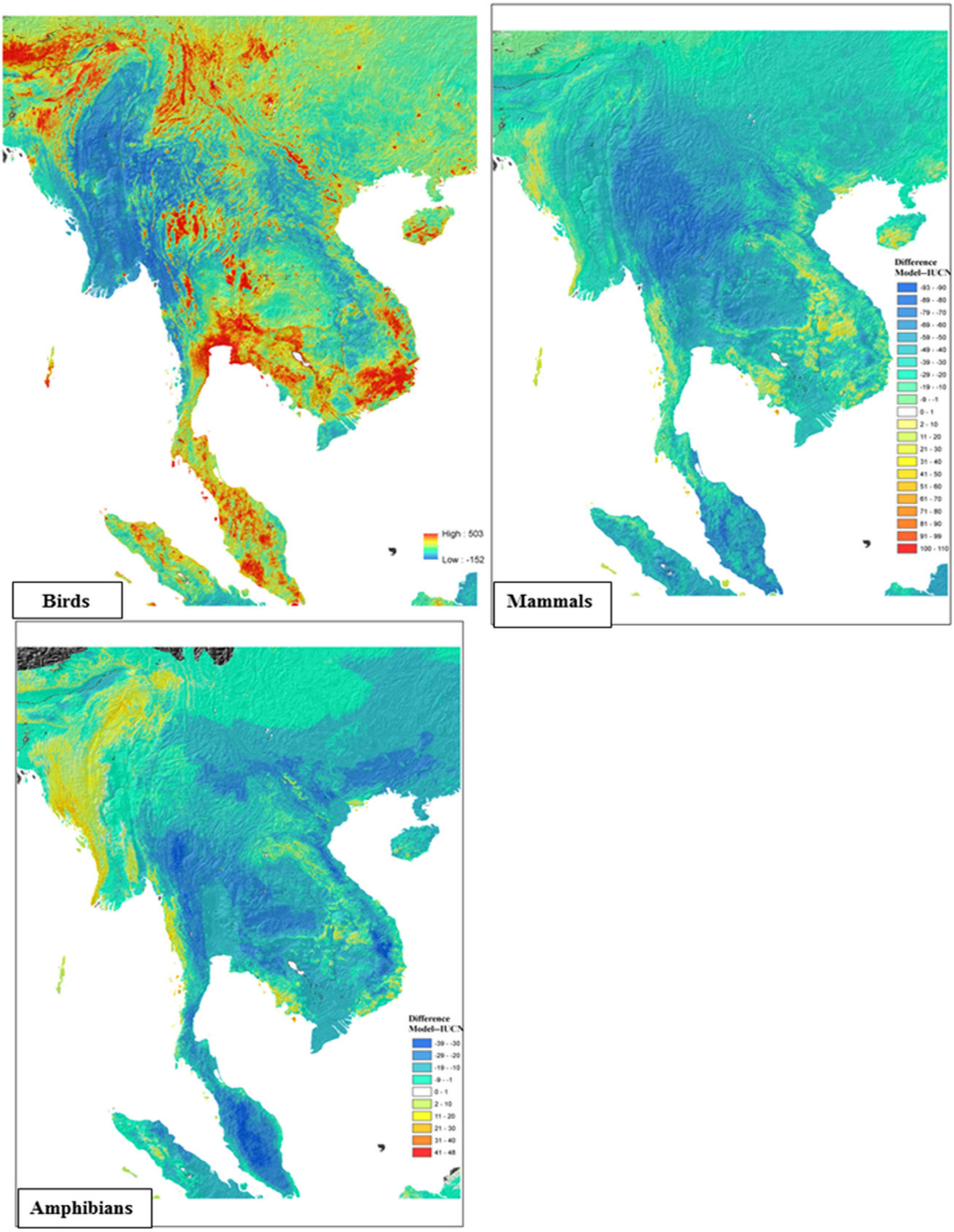

Fig. 2. IUCN-model difference: Blue-greens indicate where IUCN maps predicted more species than model analysis, whereas reds-yellows represent areas where models predict more species than the IUCN. Grey/white indicates equal numbers of species and hillshaded areas denote no species of the taxa in those regions.

region. Though almost 50% of the most diverse areas (>75% of maximum diversity) for mammals, and 55% of amphibian hotspots fall within protected areas (Table 1), this decreases to only around 10% for reptiles, and around 20% for birds and non-flowering plants. Levels of protection at a >50% biodiversity level also vary markedly, with under 50% of these regions protected for all groups and as little as 13.5%

Table 1
Percentage of hotspots protected, diversity hotspots are defined as areas with at least 50%, and 75% of maximum biodiversity for each taxa.

Hotspots	50% protected	75% protected
Mammal	37.34	49.59
Reptile	13.46	10.20
Amphibian	33.78	55.49
Aves	32.90	19.51
NF plants	30.2	23.9

protected for reptiles. This under-representation of reptiles and reptile hotspots within protected areas is likely to be because of the dominance of records from Myanmar, where only 9.5% of the land is currently protected.

When protection is examined at species level coverage is also low for the majority of species (Fig. 4). Amphibians have the largest proportion of their ranges within protected areas at 24% on average, whereas this drops to 23% in mammals, 17.9% in birds and only 13.7% in reptiles. At a family level the least well protected group (with at least 5 species: Supplements 10) are the anseriformes (32 species) with on average only 6.4% of their ranges within protected areas, followed by the charadiformes (81 species) only 7.6% of their ranges are protected on average. Of the forty families with at least 5 species with enough data to model species of 15.79% of bird families and 20% of reptile families have fewer than 10% of species ranges protected. 26.3% of bird families, 80% of reptile families and 10% of mammal families have 10–15% of species ranges protected (Fig. 3). Mammals are on average best protected with 20% of families having 30–40% of species ranges protected (Fig. 3; for species level data see Supplements 10).

IUCN redlist status for each taxa also makes a significant difference in the level of protection (Fig. 4), with species listed as vulnerable showing the highest level of protection for mammals and birds (33.6% and 22.2%), and only exceeded by data deficient species in amphibians (DD: 35.2%, Vu: 34.4%). Species with lower levels of vulnerability unsurprisingly show smaller proportions of their ranges within protected areas, presumably because they either occupy large ranges which expand considerably outside protected areas or because as they maybe more generalist species they are not limited to protected areas (Fig. 4). The low levels of protection seen in endangered and critically endangered species (where sufficient data exists to develop models) at on average 23.9% is more concerning, as these species may be more dependent on intact habitat and survive poorly outside reserves.

Differences in IUCN status classification (i.e. most reptiles were either under review or data deficient as little research has centred on these species; whereas there are few data-deficient birds and even in the 55 bird species “under-review” this is on the basis of taxonomic discussion between researchers rather than lack of research) make direct comparison between taxa more challenging (Supplements 10).

4. Discussion

4.1. Understanding biodiversity patterns

Model approaches provide a practicable method to explore biodiversity patterns across the landscape, however relative to IUCN maps of biodiversity a number of important issues are apparent. Firstly, due to the paucity of data for many of these species, many IUCN maps clearly have either artifactual errors, or are limited by current methodologies, and for many species more empirical methods of analysis are likely to provide more accurate and useful outcomes. Areas classified as most diverse also vary significantly between the two approaches (Fig. 2), with modelled analysis showing much smaller regions of “hyper-diversity” (0–5% of the total region), whereas the IUCN defines theses diverse areas as much broader (up to 40% of the region). This has significant impacts for conservation across taxa.

Alternative approaches to spatially prioritise areas for conservation either rely on local data, (which is likely to be unstandardized and may miss many important regions), or IUCN “expert” drawn maps. Unfortunately IUCN's expert maps are likely to miss rare and recently described species due to lack of data, and may lack the detailed information necessary to delineate a species ranges. Thus the approaches used here, based upon comprehensive surveys across the region, and combined with detailed environmental layers provide a more empirical approach to ensure species, and biodiversity is better understood through the greater insights derived through model approaches.

Disturbingly the areas where our projections differ most significantly from the IUCNs expert maps are the areas I class to have the highest levels of diversity across taxa. This and the lack of congruence in any of the diversity hotspots derived from the two approaches requires attention. Though both approaches are far from perfect, and both make assumptions about the data and include implicit uncertainties, analysis has formerly shown models to provide a more realistic reflection of species distributions (i.e. Di Marco et al., 2016). Though models developed

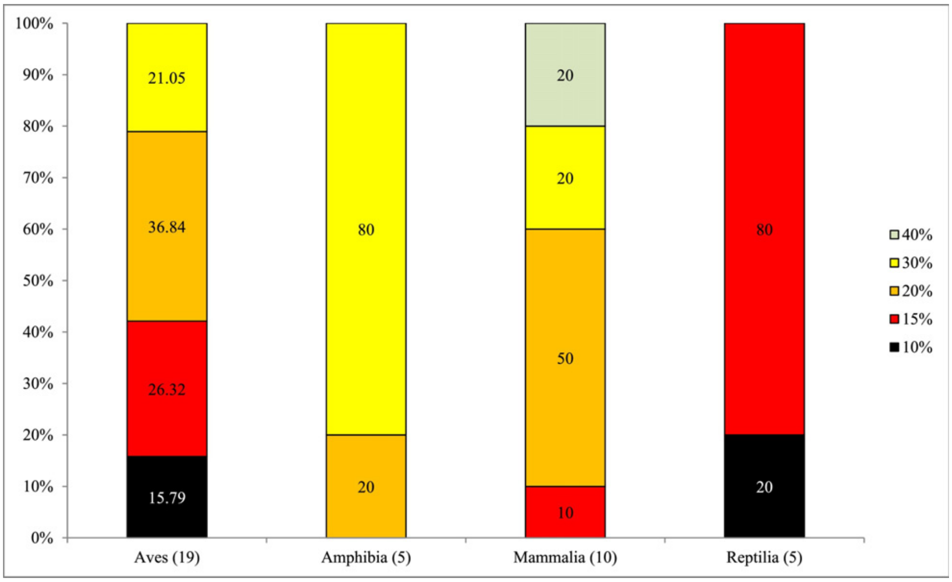

Fig. 3. Percentages of families with the percentages of species ranges protected.

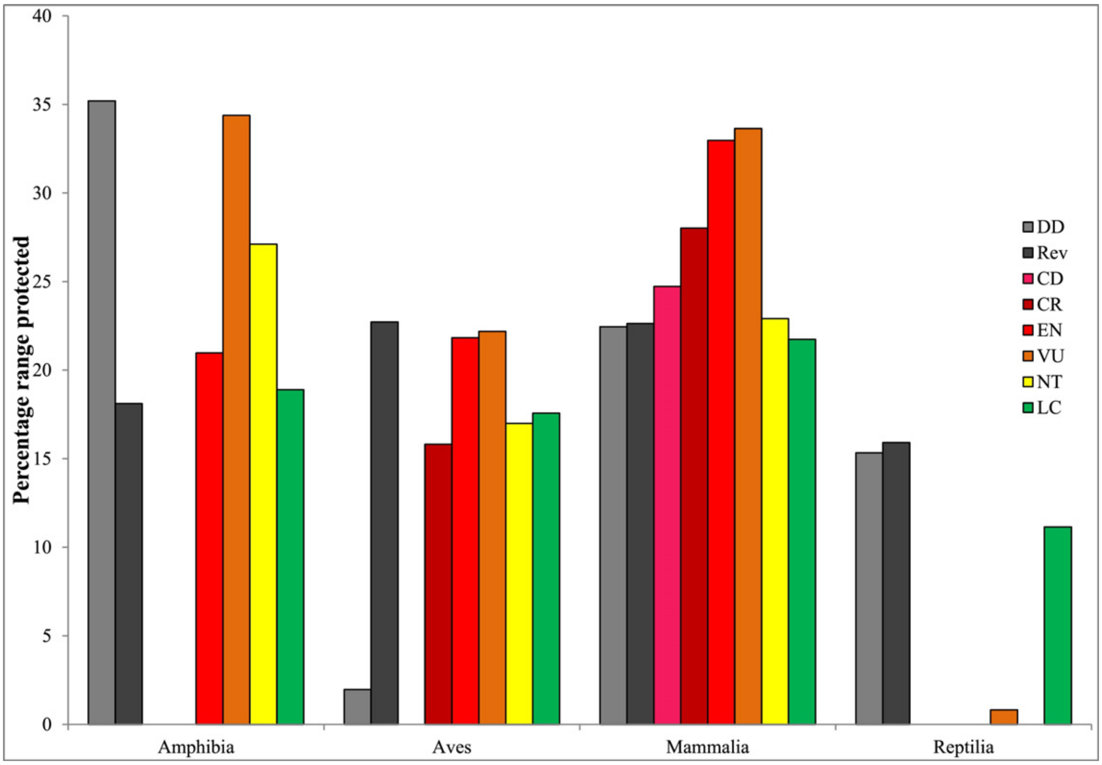

Fig. 4. Percentage of species ranges of different IUCN statuses protected on average per taxa. (DD: data deficient; Rev.: in review; CD: conservation dependant; CR: critically endangered; EN: endangered; VU: vulnerable; NT: near threatened; LC: least concern).

here do not include localised extirpation due to hunting, and may miss biogeographic factors preventing species occupying their entire "suitable range" they should still provide a reasonable reflection of species actual ranges and are likely to provide a useful basis for informing conservation and further research.

4.2. Biodiversity indicators

An often suggested solution in developing priorities to understand diversity patterns is the use of indicator taxa (Rodrigues and Brooks, 2007). However, the choice of indicators may be more a factor of what is popular, than what actually makes a good indicator species, and too few empirical studies have directly compared the correlations in diversity between different taxa across extended spatial scales (Westgate et al., 2014). Studies which have tested the congruence between biodiversity patterns of different taxa have frequently established that congruence varies taxonomically and spatially. Birds are a popular choice as an indicator group, due to their popularity, visibility, and the ease of collecting large volumes of data (Larsen et al., 2012). However, my models show that patterns of diversity even between different avian families vary markedly, and when compared overall to other vertebrate taxa the patterns of diversity differ substantially.

Interestingly these hyper-diverse regions also show relatively little overlap between taxa, despite clearly showing similarity in overall biodiversity patterns. This shows that different taxa clearly rely on different parts of the region, likely reflecting both biogeographic and human driven changes, though the limited area classified as "maximum diversity" for the region may also contribute to the low levels of congruence. However the areas predicted as most diverse for amphibians also overlapped substantially with mammals and reptiles hotspots and thus could provide a useful indicator to develop regional priorities for conservation or further research. This supports the results of other studies (i.e. Eglington et al., 2012) where bird diversity patterns have been found to correlate relatively poorly with other taxa.

Many of the studies exploring the complementarity of different taxa in providing a potential biodiversity surrogate have been limited to temperate regions (Sauberer et al., 2004; Gao et al., 2015) and though studies state that "congruence is higher closer to the equator" (Westgate et al., 2014) this to some extent fails to capture the trends in the 23.4° of tropical ecosystems on either side of the equator. Studies in the tropics which have explored these trends also found considerable differences in the biodiversity patterns of different taxa (i.e. Schuldt et al., 2015), with wide-ranging species such as carnivores found to be the worst indicators of biodiversity patterns (Andelman and Fagan, 2000; Jones et al., 2016). Multitaxa inventories and diverse approaches are therefore needed to develop conservation prioritisation measures in order to effectively conserve biodiversity across the landscape, as surrogates and indicators are unlikely to provide transferable results to inform the conservation of other taxa (Lindenmayer and Likens, 2011), though empirical methods can be used to develop surrogates on a highly regional basis (Grantham et al., 2010).

4.3. Protected area coverage

Species ranges, and biodiversity hotspots predominantly fall outside protected areas (Table 1). For reptiles in particular only a very small portion species ranges or biodiversity hotspots fall within protected areas. Consequently further efforts are needed to attempt to ensure that these hotspots are better protected, which given their relatively small areas should be possible. Average percentage of range within protected areas also peaks for intermediate levels of threat (i.e. vulnerable), whereas both highly endangered, and very common species frequently have larger proportions of their ranges outside protected areas across taxa.

Protected areas are established for a wide variety of reasons, not only reflecting biodiversity status and endemism, but also social, political and historical drivers; and consequently may not always be best positioned to protect current patterns of biodiversity and drivers of biodiversity change (McCreless et al., 2013). This may leave species and systems with low representation inside protected areas potentially vulnerable to habitat loss, or degradation, hunting, or other drivers of biodiversity loss (Hughes, 2017). Protecting areas identified here as hyperdiverse represents a simple way to ensure hotspots of diversity are adequately protected, whilst minimising the additional area of land needed to best protect biodiversity.

4.4. Effective landscape conservation approaches

Former global gap analysis has predominately relied on IUCN maps as a major tool in assessing the adequacy of current protected area coverage on a global and regional basis (Butchart et al., 2012; Cantú-Salazar et al., 2013; Venter et al., 2014; Meyer et al., 2015; Di Minin et al., 2016), yet studies clearly show the shortfalls in the methodologies and the implications in terms of regional prioritisation and species conservation status (Hughes in review; Gonzalez et al., 2016; Di Marco et al., 2016). In addition further analysis shows the dangers of range overestimation in terms of assigning correct redlist status and providing sufficient conservation have been discussed (Visconti et al., 2013; Jetz et al., 2008).

Thus developing alternate approaches which give a more precise and accurate projections of species ranges is essential to developing appropriate approaches for effective conservation (Gonzalez et al., 2016). The first step in this process may simply involve trimming IUCN distribution maps with high resolution forest cover, and appropriate altitude regions (i.e. see Li et al., 2016); but even this approach does not circumvent issues around political boundaries and species not yet assessed by the IUCN, and relies on range data and altitudinal limits which may not accurately exist for many species (Peterson et al., 2016).

Through the combination of species distribution data with appropriate environmental data it is possible to obtain a much clearer understanding of biodiversity patterns than was previously available. These modelling approaches, when applied carefully have been shown to be a reliable method to interpolate biodiversity across the landscape (Valerio et al., 2016), thus circumventing the need for extensive collection data whilst still providing reliable information on biodiversity patterns.

As stated previously the use of indicator species in assaying biodiversity patterns has been widely found to not produce informative comparisons with other taxa, and therefore to effectively develop priorities for conservation it is necessary to include multiple taxa, and then develop taxa specific priorities. This does not completely negate former approaches based upon expert knowledge to delineate species ranges and requirements, but may subsume these approaches to properly develop models which consider appropriate data at an appropriate resolution, and sensitively interpret and validate the results. Often ecological models have been criticised for a naïve approach to model development, and a lack of rigour in evaluation; but a more ecological emphasis based upon expert knowledge can facilitate the development of more accurate and relevant analysis of biodiversity based on accurate data on a species level (Searcy and Shaffer, 2016).

4.5. A better future for Southeast Asian biodiversity

Southeast Asian biodiversity is under threat, yet for the majority of species, and biodiversity overall current protected areas do not offer adequate protection. Until recently the lack of data prevented any large-scale detailed analysis on regional biodiversity patterns, making evaluating the efficiency and adequacy of protected areas impossible. Though IUCN range maps offer hope of more targeted approaches, the lack of information to inform species range maps make these maps inadequate to inform conservation at a regional scale.

However, the growing availability of various forms of data both providing high resolution data on various facets of the environment, and growing volumes of species data through online databases and citizen gathered information facilitates the development of modelling approaches to provide a more refined approach to accurately project species ranges, and therefore map biodiversity patterns. Not only does this allow protected area coverage and threats to be better understood, and inform management, but the drivers of distributions can also be determined, providing a means to better informed proactive conservation and management.

Here I show that surrogates and indicator species provide fairly limited transferable information in terms of congruence with other taxa, and that effective targeting of conservation is likely to require multi-taxa inventories and evaluation. Furthermore, many areas of maximum diversity involve the protection of areas between current protected areas, thus protecting these areas would also increase regional connectivity and provide additional conservation benefits, especially for the conservation of large ranging species.

Interestingly I also show that the proportion of species with different levels of threat is not constant, but increases in many biodiversity hotspots, and for many species in Northern Southeast Asia, where species may have naturally low densities and require special eco-physiological adaptations to survive.

To better protect diversity of the region into the future, in addition to more complete inventories and surveys for reptiles, and for many mammals; and further efforts made to share distribution data we also need to ensure that species and hotspots are better protected. Here I show spatial priorities to protect areas with the greatest number of species, and similar approaches are applicable to endangered and data deficient species, to target protection to hotspots of more threatened species (Fig. 1).

Reptiles in particular are in urgent need of regional protection, with the highest number of species "in review" (Fig. 4), the lowest levels of protection (Fig. 3), and the lack of any IUCN maps for the majority of species, research and targeted conservation is needed to secure species survival into the future. Intact forested areas of Myanmar have the lowest levels of protection, and many species in this region is likely to fall outside current protected areas; providing a regional priority for research and conservation. Following this forested regions in Lao, Vietnam and Cambodia, and especially Lao Cai in Northern Lao currently include many unprotected hotspots for regional biodiversity and endemism.

Without protection many of these regions will see the loss of forests, and increased hunting due to infrastructural growth and increased accessibility. Thus to best protect biodiversity, and the survival of species in the region depends on ensuring that current hotspots are effectively protected; and that assessments such as this become a routine part of developing regional priorities for conservation and management.

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